

# Pteronotus quadridens. By Armando Rodríguez-Durán and Thomas H. Kunz

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## Pteronotus Gray, 1838

*Pteronotus* Gray, 1838:500. Type species *Pteronotus davyi* Gray, 1838, by monotypy.

*Chilonycteris* Gray, 1839. Type species *Chilonycteris macleayii* Gray, 1839, by monotypy. Used as a subgenus by Smith (1972).

*Lobostoma* Gundlach, 1840:357. Based on *Lobostoma cinnamomeum* Gundlach, 1840, and *Lobostoma quadridens* Gundlach, 1840, by subsequent designation (Smith, 1972:55-56).

*Phyllodia* Gray, 1843:50. Type species *Phyllodia parnelli* Gray, 1843, by monotypy. Used as a subgenus by Smith (1972).

*Dermotus* Gill, 1901:177. Replacement name for *Pteronotus* Gray, 1838, erroneously believed to be preoccupied by *Pteronotus* Rafinesque, 1815, a *nomen nudum* (Miller, 1905).

**CONTEXT AND CONTENT.** Order Chiroptera, Family Mormoopidae, Subfamily Chilonycterinae. There are three subgenera, *Phyllodia*, *Chilonycteris*, and *Pteronotus* (Smith, 1972). The genus *Pteronotus* contains six species. The following is a key to these species (based on Smith, 1972, and Silva Taboada, 1979):

- 1 Wing membrane fused on middorsal line ..... 2  
Wing membrane not fused on middorsal line ..... 3
- 2 Length of forearm <50 mm ..... *P. davyi*  
Length of forearm >50 mm ..... *P. suapurensis*
- 3 Antero-medial edge of ear pinnae smooth, length of forearm >50 mm ..... *P. parnelli*  
Antero-medial edge of ear pinnae with tooth-like serrations, length of forearm <50 mm ..... 4
- 4 Nostril without lateral spikes; prominent rostral tubercle on top of muzzle ..... *P. personatus*  
Nostril with lateral spikes, low rostral tubercle on top of muzzle ..... 5
- 5 Length of mandible, 9.0-10.1 mm; length of forearm >41 mm; margin above nostril smooth and rectangular ..... *P. macleayii*  
Length of mandible, 8.0-9.1 mm; length of forearm <41 mm; margin above nostril lobulate and slightly convex ..... *P. quadridens*

## Pteronotus quadridens (Gundlach, 1840)

### Sooty Mustached Bat

*[Lobostoma] quadridens* Gundlach, 1840:357. Type locality "Cafetal St. Antonio el Fundador," Canimar, Cuba.

*Chilonycteris fuliginosa* Gray, 1843:20. Type locality "Hayti," restricted to Port au Prince by Dobson (1878:450).

*Chilonycteris quadridens* Wagner, 1855:678, name combination.

*Chilonycteris macleayii inflata* Rehn, 1904:190. Type locality "Cueva di Fari, near Pueblo Biejo, Porto Rico."

*Chilonycteris torrei* G. M. Allen, 1916:4. Type locality "La Cueva de la Majhana, Baracoa, Cuba."

*C[hilonycteris]. inflata*: G. M. Allen, 1916:6, name combination.

*C[hilonycteris fuliginosus]. torrei*: G. M. Allen, 1917:168, name combination.

*Chilonycteris fuliginosus inflata*: Anthony, 1918:244, name combination.

*Chilonycteris fuliginosus fuliginosus*: Smith, 1972:85, name combination.

*Pteronotus fuliginosus torrei*: Smith, 1972:86, name combination.

*Pteronotus quadridens quadridens*: Silva Taboada, 1976:7. First use of current name combination.

*Pteronotus quadridens fuliginosus*: Silva Taboada, 1976:7, name combination.

**CONTEXT AND CONTENT.** Two subspecies are recognized (Silva Taboada, 1979).

*P. q. fuliginosa* (Gray, 1843:20), see above.

*P. q. quadridens* (Gundlach, 1840:357), see above.

**DIAGNOSIS.** *Pteronotus quadridens* is the smallest species of the genus. It can be readily separated from its most closely related congener, *P. macleayii*, in having a smaller forearm length (<41 mm) and a smaller condylobasal length, averaging <13.6 mm (Smith, 1972). *P. quadridens* also has a shorter, narrower rostrum than *P. macleayii*. A field key, based on differences in forearm length, is useful for distinguishing these and other Antillean taxa (Baker et al., 1984). As compared with *P. quadridens*, the forearm length of *P. macleayii* >41 mm.

**GENERAL CHARACTERS.** The body is fully furred with naked wing and tail membranes (Fig. 1). The terminal 25% of the tail is free. Color ranges from grayish brown to yellowish brown, with some individuals reaching an orange-brown phase. Color phases may reflect age differences, or bleaching effects due to potentially high concentration of ammonia in the roost. Dorsal hairs are tricolored, with a grayish-white central band and dark basal and apical bands. Ventrally, the hairs are bicolored with a dark-brown basal band and grayish-white apical band (Silva Taboada, 1979; Smith, 1972).

The labionasal plate is moderately complex, lacking a noseleaf, but having cutaneous flaps covering the nostrils and three to four wart-like tubercles (not prominent) above each nostril (Smith, 1972). Ears are relatively long, narrow, and pointed, connected by two extremely low, inconspicuous ridges that fuse at the top of the nose, widening abruptly into an ample conch at the base, but well separated above the head (Silva Taboada, 1979; Smith, 1972). Three to four tooth-like serrations are present on the antero-medial edge of the long, lanceolate portion of the ear. The tragus is long and spatulate with a prominent secondary fold; it is sparsely covered with short bristle-like hairs having longer hairs on cranial and distal edges (Smith, 1972). Body mass ranges from 3 to 6 g with an average of 4.7 g in Cuba ( $n = 216$ ; Silva Taboada, 1979) and 5.6 g in Puerto Rico ( $n = 32$ ; Rodríguez-Durán, 1984).

The profile of the skull is relatively flat and the rostrum is slightly elevated (Fig. 2); the forehead rises abruptly onto a round, high braincase. The rostrum is approximately the same length as the braincase. There is a marked diastema between the outer, upper incisor and canine. The inner incisors are distinctly bifurcate. The lower incisors are reduced in size and trilobed with short, rounded heels. The dental formula is  $i\ 2/2, c\ 1/1, p\ 2/3, m\ 3/3$ , total 34. No dental anomalies were reported for *P. quadridens* by Phillips and Jones (1968), but Smith (1972) found one specimen from Jamaica with an extra left upper incisor.



FIG. 1. Female *Pteronotus quadridens* from Aguadilla, Puerto Rico.



FIG. 2. Dorsal, ventral, and lateral views of the cranium and lateral view of the mandible of *Pteronotus quadridens* from Sosua, Santo Domingo, Dominican Republic (male, Harvard University, Museum of Comparative Zoology, MCZ 16469). Greatest length of skull is 14.3 mm.

In both external and cranial size, *P. q. quadridens* is smaller than *P. q. fuliginosus* (Smith, 1972). Selected external and cranial measurements (sample sizes in parentheses) of *P. q. quadridens* are from Silva Taboada (1979) unless otherwise noted: length of forearm, 35.9–38.5 (30); zygomatic breadth, 7.1–7.7 (15); rostral breadth, 5.8–6.1 (15); length of maxillary tooththrow, 5.6–6.0 (15); condylobasal length, 12.8–13.4 (15); depth of cranium, 6.4–7.2 (15; Smith, 1972); and greatest length of skull, 13.8–14.9 (129). Selected external and cranial measurements (extremes and sample sizes) for *P. q. fuliginosus* are from Smith (1972) as follows: length of forearm, 30.1–40.8 (52); zygomatic breadth, 7.3–7.9 (35); rostral breadth, 5.9–6.4 (35); length of maxillary tooththrow, 5.8–6.2 (36); condylobasal length, 13.2–14.1 (34); and depth of cranium, 6.7–7.7 (34). There is a distinct tendency for the forearm length and greatest length of skull to increase clinally from west to east in Cuba. Males are significantly larger than females in the greatest length of skull, but females have a significantly longer forearm.

**DISTRIBUTION.** *Pteronotus quadridens* is endemic to Puerto Rico, Hispaniola, Cuba, and Jamaica (Fig. 3). *P. q. quad-*

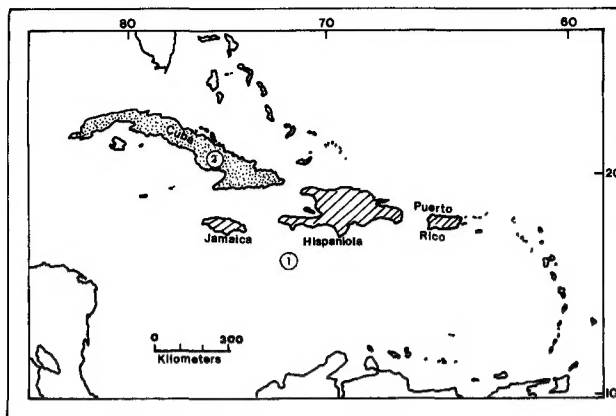


FIG. 3. Map of the Greater Antilles showing the distribution of *Pteronotus quadridens*: 1, *P. q. fuliginosus* (hash lines); and 2, *P. q. quadridens* (stipple).

*ridens* occurs only on Cuba and *P. q. fuliginosus* occurs on the three other islands (Silva Taboada, 1976; Smith, 1972).

**FOSSIL RECORD.** All fossils of *P. quadridens* known from the Antilles are believed to be from the late Pleistocene or Holocene. Fossils are known from several deposits in Masones and Jaguey caves, Cuba. The older layers are probably of late Pleistocene age. Cranial, mandibular, and humeral measurements suggest that individuals in late Pleistocene deposits were significantly smaller than those from Holocene deposits (Silva Taboada, 1974). Fossils of about the same age also are known from Cueva Grande de Judes (Woloszyn and Silva Taboada, 1977), as well as from caves in Matanzas and Camaguey, Cuba (Silva Taboada, 1979). The ancestors of *P. quadridens* most likely originated from the Central American mainland (Baker and Genoways, 1978).

**FORM AND FUNCTION.** The structure of the ulna of *P. quadridens* resembles that of *P. parnelli*, but the articular surface is reduced and the olecranon is longer in *P. quadridens*. Relative to the length of the radius, the ulna is longer than in *Mormoops* but shorter than in *P. parnelli*. The facet of the proximal surface of the radius that articulates with the trochanter of the humerus is greatly enlarged, and the curvature of the radius is pronounced (Vaughan and Bateman, 1970). The calcareus is long and slender, the femur is nearly as long as the tibia and both are slender. The wing membrane and uropatagium are attached to the ankle by way of a long ligament that is tightly bound to the distal one-half of the tibia. Wing-loading ranges from 5.6 newtons/m<sup>2</sup> for males to 5.2 newtons/m<sup>2</sup> for females (Silva Taboada, 1979). *P. quadridens* shows a reduction in size of the brachialis, extensor digitorum communis, palmaris longus, flexor carpi radialis, and flexor digitorum profundus muscles (Vaughan and Bateman, 1970).

One *P. quadridens* with non-albinistic white coloration (leucism) in the wings was observed in Puerto Rico (A. Rodríguez-Durán, pers. obs.).

**ONTOGENY AND REPRODUCTION.** *Pteronotus quadridens* is monoestrous and uniparous, with only one incidence of twinning reported (Silva Taboada, 1979). Based on testicular size, copulation begins in January. Pregnant females of *P. quadridens* have been reported from February through June (Silva Taboada, 1979). An examination of 578 females collected in Cuba from January to December (Silva Taboada, 1979) and 947 specimens examined in Puerto Rico from March to September (Rodríguez-Durán, 1984), indicate that most females are pregnant during May. Pregnant females also have been taken during May in Haiti (Klingener et al., 1978). Lactation occurs from June through September and peaks in July. Pregnant females undergo an increase in body mass of 38% from April to June. The largest embryo reported for this species weighed 1.8 g or 30.2% of the female's body mass. Newborn young form dense clusters of 50–200 individuals in shallow depressions of cave walls. Young bats are not carried by their mothers during foraging bouts (Silva Taboada, 1979).

During the breeding season, especially from April through August, either males or females may disappear completely from

established roost sites (Silva Taboada, 1979). A marked shift in the adult sex ratio, favoring females at maternity caves in Puerto Rico, has been observed during May and June (Rodríguez-Durán, 1984). These changes suggest that sexual segregation occurs during the maternity period, although Silva Taboada (1979) found no segregation of adult sexes in some Cuban caves during this period.

**ECOLOGY.** *Pteronotus quadridens* is known exclusively from caves and is one of the most abundant bats in Cuba and Puerto Rico. Together with *Phyllonycteris poeyi*, it is the most common bat species occupying hot caves in Cuba (20 out of 28 caves examined). Silva Taboada (1979) noted that most colonies of *P. quadridens* in Cuba range from 5,000 to 15,000 bats. Rodríguez-Durán and Lewis (1987) estimated that one cave in Puerto Rico housed about 141,000 individuals. In Jamaica, *P. quadridens* was observed in only one of 13 caves, with an estimated colony size of <1,000 (Goodwin, 1970).

In Cuba where *P. quadridens* has been observed in hot caves, the temperature may reach 39.6°C with relative humidity approaching 99%. In other caves, temperatures varied from 26 to 30°C and relative humidity ranged from 85 to 99% (Silva Taboada, 1979). One cave in Puerto Rico had an average daily temperature of 35°C (Rodríguez-Durán, 1984). The types of day roosts occupied by *P. quadridens* (Rodríguez-Durán and Lewis, 1987; Silva Taboada, 1979) are consistent with the reported sensitivity of mormoopids to low ambient temperature (Novick, 1963).

*Pteronotus quadridens* can be found in caves associated with (but spatially separate from) *Phyllonycteris poeyi*, *Brachyphylla nana*, *B. cavernarum*, *Erophylla sezekorni*, *Monophyllus redmani*, *Mormoops blainvillii*, *Pteronotus parnelli*, and *P. macleayii* (Goodwin, 1970; Rodríguez-Durán and Lewis, 1987; Rodríguez and Reagan, 1984; Sampedro-Marin et al., 1977; Silva Taboada, 1979). In an analysis of the relative dehydration rate of Cuban bats, Silva Taboada (1979) found that the wings of three out of 16 species tested (*Natalus lepidus*, *Mormoops blainvillii*, and *Pteronotus macleayii*) dehydrated faster than *P. quadridens*. Each of these species typically roost in hot, humid caves.

*Pteronotus quadridens* shows evidence of temporal separation from other species occupying the same cave (Rodríguez-Durán and Lewis, 1987; Sampedro-Marin et al., 1977; Silva Taboada, 1979). This bat is the first to leave the cave at dusk, usually beginning 11 min before to 10 min after sunset. The bats exit in well-formed columns and may fly into the open or through corridors of trees. Most of the return activity occurs from 17 min before to 10 min after sunrise, although some individuals may return <1 h after sunrise. Movements of bats in and out of the cave continue throughout the night, but there is only one major exit and return at dusk and dawn, respectively. It is not clear whether these bats have one or two periods of feeding activity each night. If there are two periods of activity, some bats may use night roosts outside the cave (Silva Taboada, 1979).

A column of departing *P. quadridens* in Cuba was followed for 7 km before it disappeared from view (Silva Taboada, 1979). In Puerto Rico, some individuals from one colony dispersed up to 9 km to reach their feeding grounds (Rodríguez-Durán, 1984). In a test of homing ability, individual *P. quadridens* were able to return to their roost on the night of release from distances up to 30 km (Silva Taboada, 1979).

The early departure behavior of some *P. quadridens* makes them susceptible to predation by diurnal birds. American kestrel (*Falco sparverius*), Red-tailed hawk (*Buteo jamaicensis*), and wintering merlins (*Falco columbarius*) attempt to capture *P. quadridens* during nightly emergence flights (Rodríguez-Durán, 1984). Red-tailed hawks generally were not successful in capturing bats, but merlins regularly preyed on *P. quadridens*; this predation pressure appeared to influence nightly emergence flights (Rodríguez-Durán and Lewis, 1985). Specimens of this bat have not been recovered from owl (*Tyto*) pellets in Cuba (Silva Taboada, 1974). In addition to birds, feral house cats (*Felis sylvestris*) may be the most important predator of *P. quadridens*. Rodríguez-Durán (1984) and Rodríguez and Reagan (1984) observed groups of feral cats hunting for bats at cave openings. As many as two to five cats have been observed near cave openings at times of greatest activity (departure and return) and have captured bats as they passed by. Both reports of cat predation were incidental and there was no indication which species of bat the cats actually captured since more than one species was present in the cave. Snakes, including boas (*Epicrates inornatus*,

Rodríguez and Reagan, 1984; *E. angulifer*, Hardy, 1957), use hunting strategies similar to those of cats at cave entrances. Both species of snakes are known to capture bats in caves inhabited by *P. quadridens*, although it is not known whether this species has actually been captured by snakes.

*Pteronotus quadridens* feeds on flying insects captured primarily in the forest understory. Based on the analysis of 195 stomach contents taken between January and December in Cuba, 75% contained coleopterans, 41.2% dipterans, 17.6% lepidopterans, 16.2% orthopterans, 13.2% homopterans, and <1% other (hymenopterans, dyctiopterans, dermapterans, and heteropterans; Silva Taboada, 1979). Similarly, an examination of 158 fecal samples from Puerto Rico (June through September) revealed that 47.5% of the samples contained coleopterans, 48.1% lepidopterans, 9.5% hymenopterans, 26.6% dipterans, 27.9% hemipterans, and 20.3% homopterans (Rodríguez-Durán and Lewis, 1987). Remains of one to seven different insect families have been reported from one individual (Rodríguez-Durán, 1984; Silva Taboada, 1979), suggesting that this bat is a dietary opportunist. Additionally, up to 10.7% of the samples contained pollen (Rodríguez-Durán and Lewis, 1987). Silva Taboada (1979) also found pollen grains in the stomach of one bat. We suspect that *P. quadridens* inadvertently consumes pollen as it ingests insects, which carry pollen, rather than feeding directly on nectar and pollen.

Average nightly food consumption was 1.25 g (24.8% of body mass,  $n = 129$ ) for males and 1.12 g (23.0% of body mass;  $n = 119$ ) for females (Silva Taboada, 1979). The amount of food ingested increased by 20% from winter to summer, but because body mass also increased during this period, the relative increase in nightly food consumption averaged 11%. Feeding activity occurs nightly even when ambient temperature is as low as 8°C (Silva Taboada, 1979). Body (rectal) temperature of *P. quadridens* during nightly foraging bouts increased from 35.3°C in winter (November–April) to 37.8°C in summer (May–October; Silva Taboada, 1979;  $n = 497$ ). Significant differences in body temperature have been observed in relation to sex and time of day; body temperature is higher in females than males and is lower upon return from feeding (Silva Taboada, 1979).

Several species of parasites are known from *P. quadridens*. These include seven trematodes *Ochoterenatrema diminutum*, *Acanthatrium*, *Urotrema scabridum* (Silva Taboada, 1979), *Parabascus silvai*, *Postorchigenes insulans*, *P. cubensis*, and *Limatulum solitarium* (Odening, 1973); one cestode *Vamirolepis* (Silva Taboada, 1979); seven nematodes *Physiocephalus sexalatus*, *Spirocerca lupi*, *Physalioptera*, *Capillaria* (Silva Taboada, 1979), *Torrestrongylus torrei*, *Histiogstrongylus coronatus*, and *Physiocephalus* (Barus and del Valle, 1967); one acanthocephalan *Prostemonorchis novelai* (Silva Taboada, 1979); six mites *Chirotonyssus cubensis*, *Steatonyssus ceratognatus* (Dusbabek, 1969), *Cameroniella torrei* (Dusbabek, 1967a), *Eudusbabekia saquei* (Dusbabek, 1967b), *Lawrenceocarpus micropilus* (Dusbabek and Cruz, 1966), and *Antricola silvai* (Cerny, 1967); two ticks *Ornithodoros vigerasi* and *Parantricola marginatus* (Cerny, 1969); and two bat-flies *Trichobius dusbakeki* and *T. frequens* (Peterson and Hurka, 1974).

**GENETICS.** *Pteronotus quadridens* has a diploid number (2n) of 38 chromosomes and a fundamental number (FN) of 60 chromosomes (Baker and Bickham, 1980). The karyotype of *Pteronotus* consists of six large and four medium-sized metacentric or submetacentric autosomes, two large, and four small acrocentric autosomes, and two small submetacentric autosomes. The X chromosome is submetacentric and the Y is acrocentric (Sites et al., 1981). Patton and Baker (1978) suggested that *Pteronotus* and *Noctilio* share a common ancestor that has a primitive 2n = 36, FN = 60, and that these two genera are more closely related to each other than either is to phyllostomids. No differences in G-band patterns among the *Pteronotus* species have been reported, suggesting that chromosomal changes within the Mormoopidae have been conservative (Sites et al., 1981).

**REMARKS.** Silva Taboada (1976) concluded that the bat described as *Lobostoma quadridens* by Gundlach (1840) was the same species later described by Gray (1843) as *Chilonycteris fuliginosa*. Silva Taboada (1976) based his conclusion on examination of 220 adult specimens of the two species in question (*C. macleayii* and *C. fuliginosa*), including the original collection sent to Germany by Gundlach and a reinterpretation of Gundlach's description. Ac-

cording to Silva Taboada (1976) the only specimen in Gundlach's collection that is cataloged as "*Chilonycteris quadridens* Type" is without doubt the smaller of the species. Smith's (1972) cluster and three-dimensional phenetic analyses of mormoopid species, based on selected external and cranial measurements, revealed that *P. quadridens* is most similar to *P. macleayii*; the greatest phenetic distance coefficient between these to insular taxa was 0.40.

The generic name *Pteronotus* is of Greek derivation combining the words *pteron* meaning wing and from the Latin word *otos* which means pertaining to (Brown, 1954). The specific name *quadridens* is a derivation from Latin combining the word *quatri* meaning four and *dens* meaning tooth (Woods, 1944).

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